

A CLARIFICATION OF THE STATUS OF CAREX CRINITA AND C. GYNANDRA (CYPERACEAE)

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Abstract. *Carex crinita* and *C. gynandra* are considered by some authors to be conspecific on the basis of morphological similarities. Variation in morphology, foliar anatomy, chromosomal numbers, and habitat preference among 12 populations of these taxa was studied to clarify their status and relationship. Two groups of populations are distinguished by non-overlapping qualitative differences in the morphology of perigynia, scales and sheaths. These groups appear to be reproductively isolated by differences in flowering time where they are sympatric. These taxa must be considered as distinct species on the basis of the morphological differences and reproductive isolation. Shared features of morphology, anatomy, and chromosomal number suggest that they are very closely related.

Carex is the largest and most complex genus of the Cyperaceae in temperate regions. Estimates of numbers of species range from 793 (Kükenthal, 1909) to 1500 (Airy-Shaw, 1973). Existing classifications of this taxonomically difficult group are based on the morphology of features which appear to be highly reduced and conservative. The plants are monoecious and anemophilous. A pistillate flower consists of a uniovulate gynoecium and a single style with 2 to 3 stigmas, and is included in a modified bract called a perigynium which is subtended by a single scale. The linear leaves are ligulate and have a closed tubular sheath. Variation in relatively few characters, such as the shape, size, and color of the perigynia and subtending scales, the dimensions of leaves and of involucre bracts, and differences in habit are used to distinguish species, although the extent and pattern of variation of these characters is often not understood. Various authors have used species concepts which are narrow (MacKenzie, 1935) or broad (Fernald, 1950) with regard to morphological variation. The construction of a classification of *Carex* which accurately represents the evolutionary relationships of taxa requires a more complete understanding of the patterns of variation within the genus. Morphological variation must be better understood and documented. Variations in anatomy, cytology, and reproductive biology which have been shown to be valuable in assessing relationships of taxa in the Poaceae (Stebbins & Crompton, 1961) may also be important in the Cyperaceae.

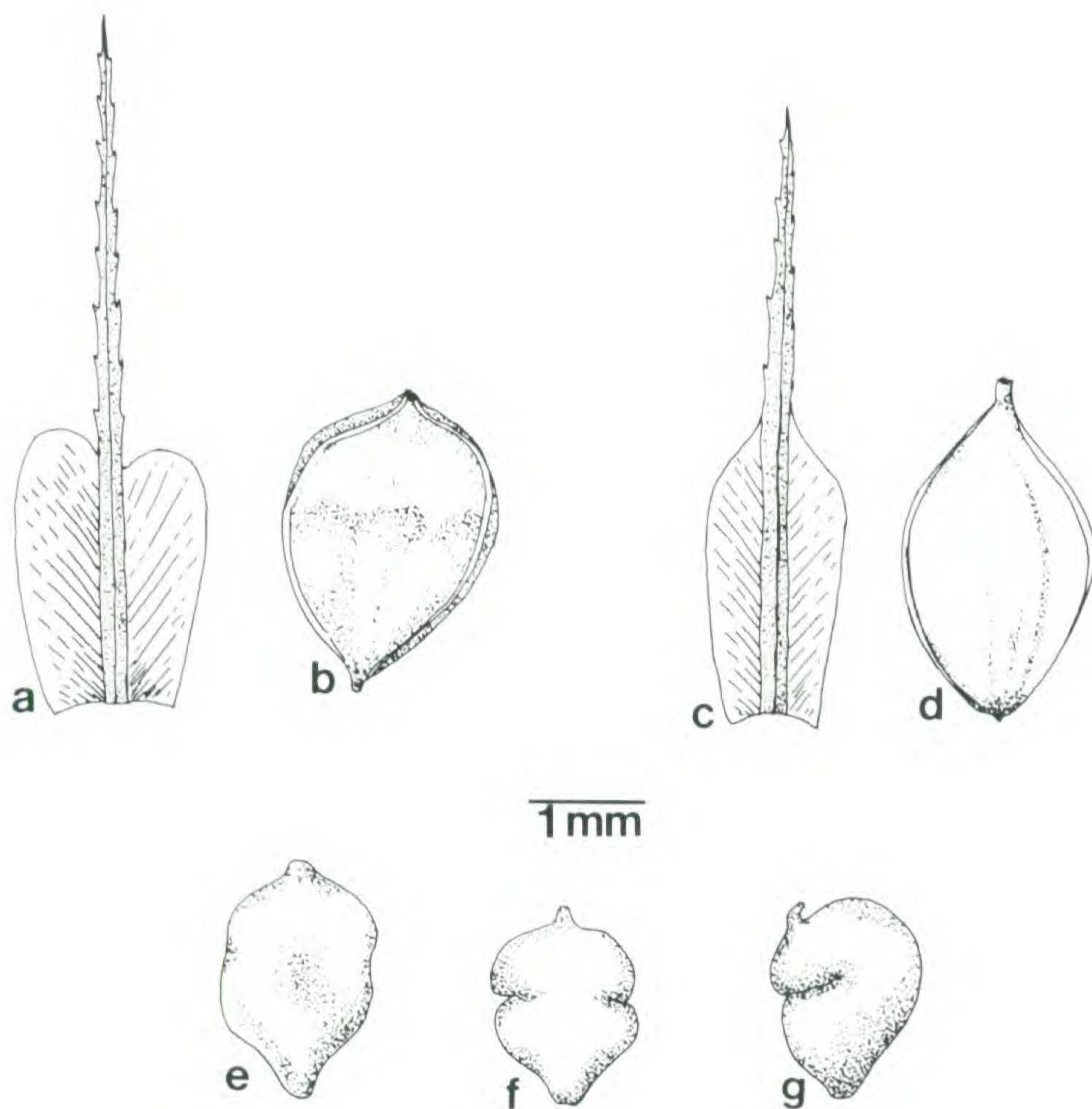


Figure 1. **Representative perigynia, achenes, and scales.** **A.** Pistillate scale of *C. crinita*. **B.** Perigynium of *C. crinita*. **C.** Pistillate scale of *C. gynandra*. **D.** Perigynium of *C. gynandra*. **E-G.** Achenes. (A, B, G; *C. crinita*, Standley 77-95; C, D; *C. gynandra*, Standley 76-104; E, F; *C. gynandra* Standley 77-76).

One specific problem which may be resolved by the application of a biosystematic analysis is the relationship of two taxa of eastern North America which are assigned to section *Cryptocarpae* (Fernald, 1950). *Carex crinita* Lam. and *C. gynandra* Schwein. are tall, caespitose perennials of wet sites, with pendant unisexual spikes, biconvex perigynia, awned scales, and lenticular achenes which are often invaginated on one margin. They were originally distinguished by differences in the shape of the perigynia (Schweinitz, 1824) and later by additional differences in the vestiture of the sheaths of the proximal leaves and the shape of the scales (Boott, 1858). These two taxa have been recognized as distinct species (Weatherby, 1923;

MacKenzie, 1935; Hermann, 1941) or as subspecies or varieties of a single, polymorphic species (Bailey, 1886; Fernald, 1950; Gleason & Cronquist, 1963). Complete descriptions and synonymy are provided by MacKenzie (1935). *Carex mitchelliana* M.A. Curtis of the southeastern coastal plain is morphologically similar to *C. crinita* and *C. gynandra*, but is distinguished by differences in the shape of the achenes. Although this taxon is undoubtedly part of the *Carex crinita* complex, its status will not be discussed at this time as populations have not been investigated in the field.

The present study is an attempt to resolve the problems of classification of these taxa by examining variation in morphology, foliar anatomy, chromosomal numbers, and habitats within populations in the vicinity of Ithaca, N.Y. This information, although from a limited geographic area, is useful in determining whether these two taxa should be recognized as separate species, and in clarifying their relationship.

METHODS

Eleven populations of *Carex* within a 20 km radius of Ithaca, N.Y. were sampled in this study (Table 1). Plants in each population were enumerated and a random sample of 10% of the plants in each population was chosen for study of morphological and anatomical features. For each character studied, average values are based on a single measurement per culm, with the following exceptions: the average of five measurements per culm was used for estimates of the dimensions of perigynia, scales, and achenes of each plant. To standardize measurements, only the proximal spike on a culm was chosen for study. Perigynia and their subtending scales were chosen arbitrarily from among those on the basal third of that spike.

Herbarium specimens at CU, BH, GH, NY, and TRT were examined for the construction of distribution maps and to test hypotheses developed in the study of populations. In addition, photographs of the holotype of *Carex crinita* (P, photo GH!) and the holotype of *C. gynandra* (PH!) were examined to verify the use of these names.

For anatomical study, a section 5 cm in length from the middle of the longest leaf of a randomly selected vegetative culm from each sampled plant was preserved in FAA. Transverse sections of leaves were cut with a razor blade, cleared in commercial bleach for 5 minutes, and mounted in Hoyer's solution for study.

Table 1. Descriptions of localities of populations of *Carex crinita* and *C. gynandra* studied in the vicinity of Ithaca, N.Y.

Population	Location	Elevation (m)	Habitat	Taxon
Connecticut Hill	Tompkins Co., 7.5 km W of Newfield	527	marsh	* <i>C. gynandra</i>
Henderson Gulf	Tompkins Co., 5 km SW of Newfield	375	marsh	* <i>C. gynandra</i>
Carter Creek	Tompkins Co., 0.5 km NE of Alpine	549	marsh	* <i>C. crinita</i>
Michigan Hollow	Tompkins Co., 5 km S of Danby	395	marsh, swamp	<i>C. crinita</i>
Spencer	Tioga Co., 2.5 km N of Spencer	330	marsh	<i>C. crinita</i>
Slaterville	Tompkins Co., 5 km N of Slaterville Springs	375	marsh	* <i>C. crinita</i> , <i>C. gynandra</i>
Six-Mile Creek	Tompkins Co., 7 km SE of Ithaca	215	marsh	<i>C. crinita</i>
Freeville	Tompkins Co., 0.5 km N of Freeville	318	marsh, swamp	* <i>C. crinita</i> , * <i>C. gynandra</i>
Sapsucker Woods	5 km N of Ithaca	325	marsh	* <i>C. crinita</i>
Lansing	Tompkins Co., 5 km W of South Lansing	335	marsh	<i>C. crinita</i>

*= chromosomal number determined for this population.

For study of chromosomes, collections of staminate spikes were made during the first half of May 1976. Spikes were fixed in Carnoy's solution (3:1 absolute ethanol: acetic acid, v/v) for at least 24 hours at 10° C, and stored in 70% ethanol under refrigeration. Anthers were squashed onto a slide and stained with acetocarmine according to the methods outlined by Faulkner (1972). Counts of chromosomes were obtained from metaphase plates of the first meiotic division of the microsporocytes. The majority of counts reported are based on at least five counts in each anther studied.

RESULTS

The majority of morphological characters studied exhibited little variation among populations or individuals. Dimensions of culms, leaves, bracts, spikes, scales, and achenes exhibit the same range of variation in both taxa (Table 2). These data were obtained from

Table 2. Morphology of *C. crinita* and *C. gynandra*

Character	<i>C. crinita</i>		<i>C. gynandra</i>	
	Mean	Range	Mean	Range
Length of vegetative leaf	117 cm	82-165	107 cm	65-148
Width of vegetative leaf	10 mm	7- 13	10 mm	7- 13
Height of flowering culm	119 cm	73-155	116 cm	67-162
Length of involucral bract	34 cm	18- 60	26 cm	12- 46
Width of involucral bract	9 mm	6- 11	7 mm	5- 13
Length of staminate spike	6.3 cm	3.8- 9.0	4.5 cm	1.5- 6.3
Length of pistillate spike	7.2 cm	4.3-11.4	7.4 cm	5.5-10.4
Length of proximal peduncle	4.5 cm	2.0- 7.2	2.9 cm	1.5- 5.6
Length of perigynium	2.5 mm	2.0- 3.0	3.1 mm	2.4- 4.2
Width of perigynium	1.8 mm	1.5- 2.0	1.7 mm	1.5- 2.1
Thickness of perigynium	1.0 mm	.8- 1.2	1.5 mm	1.3- 1.7
Length of pistillate scale	6.0 mm	3.2-10.0	5.2 mm	3.5- 8.0
Length of awn of pistillate scale	3.9 mm	1.0- 7.5	2.8 mm	1.5- 5.8
Length of achene	1.6 mm	1.3- 2.0	1.8 mm	1.6- 2.1
Width of achene	1.3 mm	1.1- 1.4	1.3 mm	1.1- 1.4
Apex of scale	retuse		acute	
Vestiture of sheaths of proximal leaves	glabrous		scabrous	
Outline of perigynium	obovate		elliptical	

study of local populations, but are consistent with dimensions of herbarium specimens from the entire range of distribution of both taxa. Achenes are lenticular in outline but margins may be entire or invaginated along one or both margins (Fig. 1). The shape of achenes has been used to distinguish taxa within this group. I have found that the shape of the fruit commonly varies among perigynia of a single individual and is therefore not a reliable taxonomic character.

Three morphological features, vestiture of the sheaths, shape of the scales, and shape of the perigynia exhibited variation between populations (Table 2). The sheaths of leaves, particularly the sheaths of the proximal leaves, are either glabrous or scabrous. Scabrous sheaths have an average of 20 silica prickles (0.15 mm in length) per mm². Plants with glabrous sheaths lack prickles entirely. The scales which subtend the perigynia have a broad, 3-nerved midrib that is excurrent as an awn. The length of this awn varies within a spike, decreasing markedly toward the apex of the spike. The scale, exclusive of the awn, is obovate in outline and may be acute or retuse at the apex (Figure 1). Perigynia may be obovate or elliptical in outline (Figure 1). Obovate perigynia are rounded in their cross-sectional outline, with a characteristic width of 1.8 mm and thickness of 1.5 mm. The average length of an obovate perigynium is 2.4 mm. Elliptical perigynia are flattened in cross-sectional outline, with an average width of 1.7 mm and thickness of 1.0 mm. These have an average length of 3.0 mm. Length of the perigynia is correlated with differences in the characters of outline and cross-sectional shape, but the range of perigynium length does overlap, as shown in fig. 2, and is not a consistently reliable taxonomic character.

Patterns of variation in the character-states of sheaths, scales and perigynia are correlated. Plants with scabrous sheaths have dorsiventrally flattened, elliptical perigynia and scales which are acute at the apex. Plants with glabrous sheaths have inflated, obovate perigynia and scales which are retuse at the apex. The scatter diagram (Fig. 2) illustrates these correlations. Two groups of populations, which correspond to the two taxa, are clearly distinguishable on the basis of these three morphological features.

Leaves are shallowly plicate (Fig. 3) with an average of 40 (range, 28–46) vascular bundles separated by transversely oblong air-

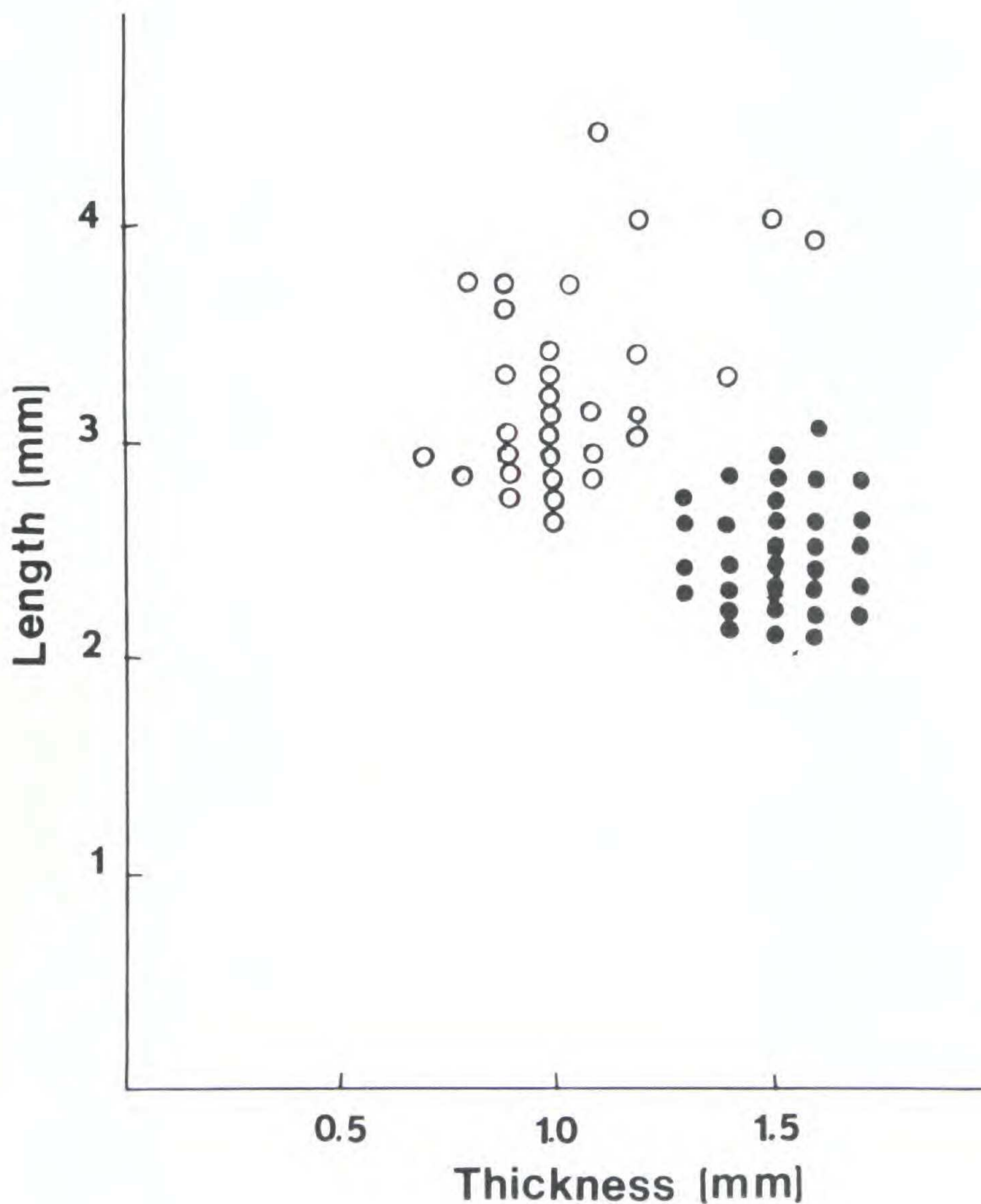


Figure 2. Scatter diagram of dimensions of perigynia. Open circles represent plants with scabrous sheaths (*Carex gynandra*). Closed circles represent plants with glabrous sheaths (*Carex crinita*).

cavities. The epidermal surfaces are differentiated. The adaxial epidermal surface consists of cells which lack papillae. Cells of the abaxial surface are smaller, and have a single median papilla. Stomates occur only on the abaxial surface. Bulliform cells occur in a single group adaxial to the midvein, and consist of a layer of large, thin-walled cells subtended by a layer of smaller clear cells. The adaxial projection of the midvein, or keel, may be rounded or acute

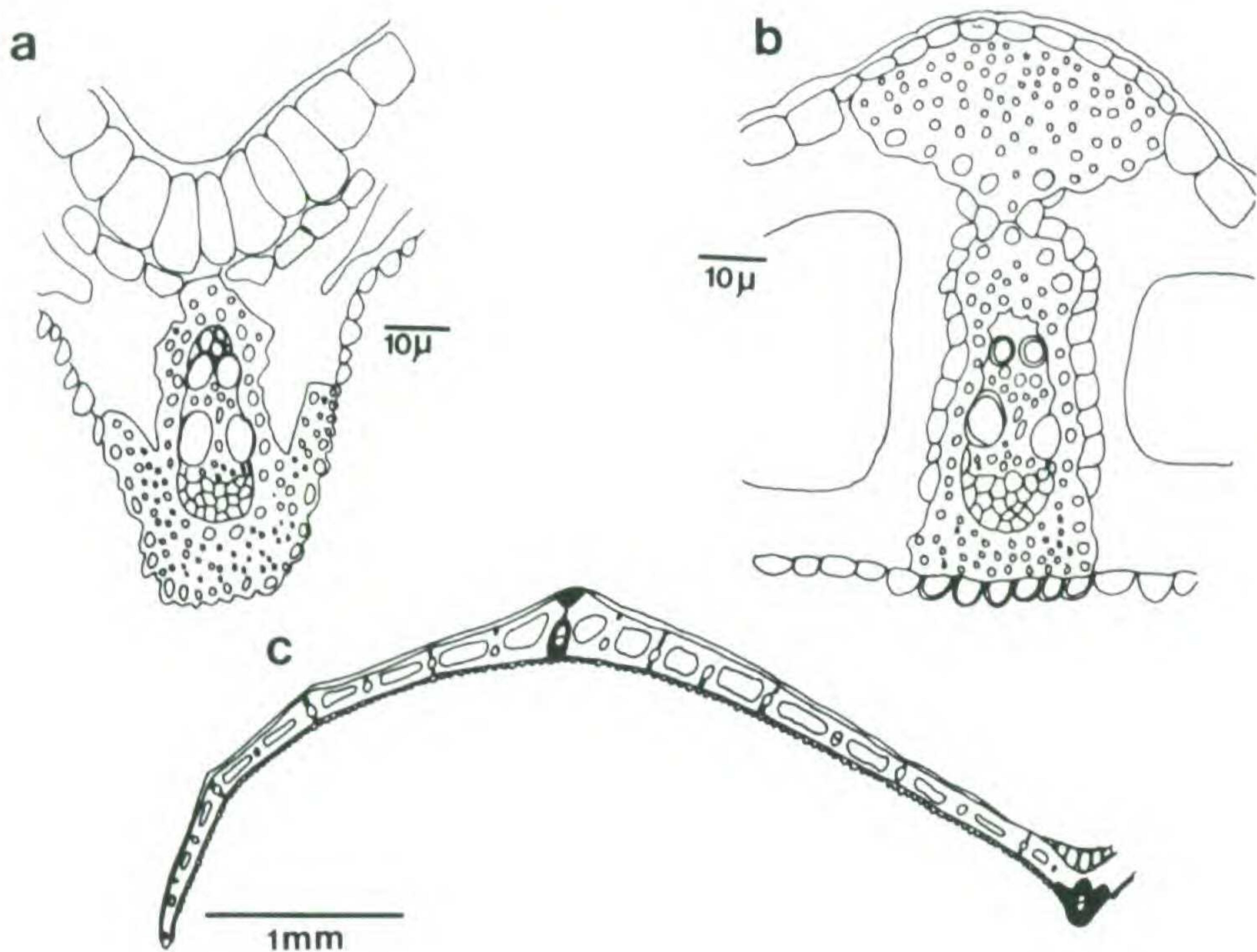


Figure 3. Features of transverse sections of leaves of *Carex gynandra* (Standley 77-76). A. Midrib, showing median vascular bundle. B. Secondary vascular bundle. C. One-half transverse section of leaf.

in transverse section. Variation in the shape of the keel was not found to be correlated with variation in other features of anatomy or of morphology. No other variations in foliar anatomy were observed.

Chromosomal numbers were obtained from five populations of plants with glabrous sheaths (Table 1). All individuals studied had 33 bivalents. No univalents or multivalents were seen, although Wahl (1940) observed both $n = 33$ and $n = 32+3$ in plants of *Carex crinita*. I examined voucher specimens for his counts at BH and GH. No morphological variation was correlated with these differences in pairing.

Populations studied in upstate New York occur in roadside ditches and in two major types of undisturbed communities with waterlogged soils. The majority of populations occurred in wet open meadows (Table 1) dominated by monocotyledons. Up to 20 species, including *Typha latifolia*, *Acorus calamus*, *Glyceria grandis*, *Scirpus cyperinus*, *Eupatorium maculatum*, *Impatiens capensis*, and *Onoclea sensibilis* frequently occur with *Carex* in these sites. Soils

are glacial silt-loams or gravels.

A few populations were located in wooded swamps dominated by *Acer rubrum*, *Alnus rugosa*, *Vaccinium corymbosum*, and *Viburnum dentatum*. Fewer than ten herbaceous species typically occur with *Carex* on hummocks in these swamps. These species include *Dryopteris cristata*, *Rubus pubescens*, *Symplocarpos foetidus*, and *Osmunda cinnamomea*. Soils tend to be organic mucky silts.

Although these two community types may be assumed to differ in environmental factors such as temperature, humidity, and the availability of light, differences in habitat were not correlated with morphological or anatomical differences in the populations of *Carex* which were studied.

Distribution maps of the two taxa (Figure 4) were constructed. Regional distribution maps are also provided by Braun (1967), Hermann (1941), Radford et al. (1968), Voss (1972), and Wheeler (1981). The two morphological forms have different ranges, although they are sympatric over a large part of the northeastern United States. *Carex crinita* occurs from Nova Scotia west to Wisconsin, and south to Georgia and Texas. It is uncommon in the mountains of the Appalachians and Adirondacks. Löve and Löve (1981) report a new record of this species from Winnepeg, Manitoba. *Carex gynandra* has a more limited geographic distribution. It occurs from Newfoundland west to the northern Great Lakes region, and south in the Appalachians to northern Georgia. This taxon generally occurs at higher elevations than *Carex crinita*, and is less common on the coastal plain.

The taxa are geographically sympatric over most of their range of distribution. Populations in central New York, however, generally consist of only one morphological form. Sympatric populations of both taxa occurred only in two locations within this region, the Slaterville and Freeville populations (Table 1). As the two taxa have the same chromosomal number, they would be expected to be interfertile (Faulkner, 1973; Standley, 1981) and to hybridize in the absence of other barriers to interbreeding. An examination of populations in these two localities yielded one individual which appeared to be intermediate in features of the scabrosity of sheaths, shape of the perigynia, and apical shape of the pistillate scales. No achenes developed on this plant, leading to the conclusion that it was a putative hybrid of reduced fertility.

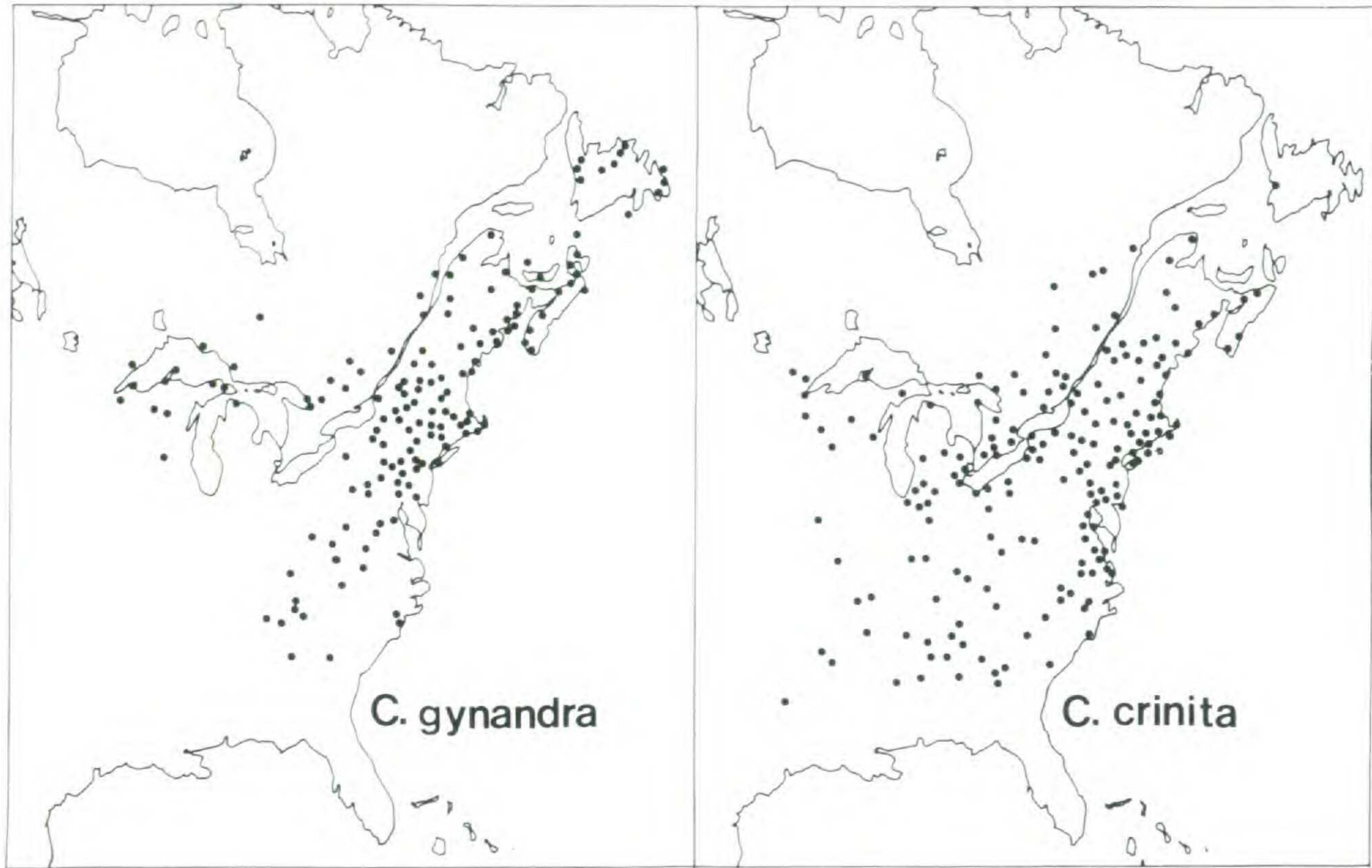


Figure 4. Distribution maps for *Carex gynandra* and *C. crinita*.

Differences in the phenology of flowering may act as isolating mechanisms in sympatric populations. Observations at the Slaterville site in May of 1977 indicated that plants with scabrous sheaths (*Carex gynandra*) initiated flowering at least one week later than plants with glabrous sheaths (*C. crinita*). This observation requires additional quantification, but suggests that there is little overlap of flowering time.

DISCUSSION

Carex crinita and *C. gynandra* do not differ with regard to most features of the morphology of leaves and of inflorescences, the anatomy of leaves, chromosomal numbers, and habitat preferences. Correlated variation in the morphology of perigynia, of pistillate scales, and of the sheaths of leaves is the basis for clustering populations in this study into two distinct taxa. These sets of characters differ in their geographical distribution, although taxa are sympatric over part of their range. These patterns of variation are consistent with those observed in systematic studies of related species of *Carex* (Standley, 1981) which are distinguished by morphological differences of the perigynia, scales, and inflorescences. Chromosomal numbers and foliar anatomy have been found to be most useful in clustering related species. Subspecies are defined as groups of populations which differ in their geographic distribution and which differ, although not consistently, in a few morphological characters. The two taxa distinguished in this study, *Carex crinita* and *C. gynandra*, are considered to be distinct yet closely related species in accordance with this model, as they differ consistently in morphology, overlap geographically, and appear to be reproductively isolated through differences in the phenology of flowering. Speculation on the process of divergence of these taxa requires additional evidence on the evolutionary polarity of the character-states which distinguish them. Current studies of the systematics of the Cryptocarpae and Acutae groups will attempt to resolve this question.

CONCLUSIONS

The study of populations of *Carex crinita* and *C. gynandra* in the vicinity of Ithaca, N.Y. has provided information on variation in

morphology, foliar anatomy, habitat, and chromosomal numbers. Details of foliar anatomy of both taxa and the chromosomal number of $n = 33$ for *Carex gynandra* are documented for the first time. Species are distinguished by the consistent correlated differences in the morphology of the sheaths of leaves, the perigynia, and the pistillate scales, and appear to be reproductively isolated by differences in the phenology of flowering. This study has demonstrated that problems of species classification in *Carex* can be resolved through a better understanding of the patterns of variation and reproductive interactions within the genus.

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